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FLOWER AND SEED OF HEDYOSMUM NUTANS[1]

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(WITH PLATES XXXIV–XXXVI)

The investigation of the seed development of *Hedyosmum* (Chloranthaceae) was undertaken at the suggestion of Professor DUNCAN S. JOHNSON. Of the 20 or more species of this genus, two species were studied. These two, *H. nutans* and *H. arborescens*, represent the largest of the three subgenera of the genus, so that the following results can perhaps be taken as characteristic of the genus as a whole. All of the figures used, except fig. 38, are from *H. nutans*. In the important features of the development of the embryo sac, perianth, etc., of *H. arborescens*, there is quite close agreement with those of *H. nutans*.

All of the material used was fixed by JOHNSON in chromo-acetic fixative.[2] The further work of imbedding, sectioning, and staining was done by the writer, except that figs. 41 and 44 were made from slides previously prepared by JOHNSON. The sections from which drawings were made were cut 7 μ thick. All sectioned material was stained with Flemming's triple stain and mounted in balsam.

The writer gratefully acknowledges the aid received from Professor JOHNSON, who inspected the slides from which drawings were made, read the manuscript, and gave helpful suggestions.

Staminate flowers

The staminate flowers arise in short conelike catkins, consisting of 100 or more flowers each, one male catkin arising beside the female inflorescence near the end of the flowering shoot. Each male flower consists solely of a single, elongated, inverted, pyramidal stamen with a microsporangium at each of its four corners.

The microsporangia possess the usual epidermis, endothecium, tapetum, and several-layered archesporium (figs. 1, 2). From the spore mother cells, tetrads of microspores are produced in the usual way (figs. 3-5). The outer wall of the microspores (exine) is roughened by closely packed peglike tubercles 1 μ long and 0.5 μ in diameter (fig. 5). There are also present over the surface of the microspore 6 unthickened meridional bands, through one of which the pollen tube emerges (fig. 6, polar view). The inner wall of the microspore (intine) consists of a darkly staining layer of cellulose (fig. 5). The mature pollen grain has the usual vegetative and generative nuclei (fig. 5).

CLARKE (5) describes the stamens of the genera *Chloranthus*, *Ascarina*, and *Hedyosmum* as being two-celled, and before opening four-celled, due to a spurious, not always complete, dissepiment in the line of dehiscence. He says:

The question referring to the structure of the anthers appears to have arisen entirely from those of *Chloranthus* itself as those of the other genera [of the family Chloranthaceae] are all of the ordinary two-celled character, or are spuriously four-celled from induplication at the line of dehiscence, a common occurrence with two-celled anthers; and in fact the four-celled structure is more apparent on a cross-section being made, both in *Hedyosmum* and *Ascarina*, especially the latter.

Neither SOLMS (12), BAILLON (1), EICHLER (6), BENTHAM and HOOKER (2), VAN TIEGHEM (13), nor ENGLER (7) refer to such peculiarity of structure as that mentioned by CLARKE. They describe the anthers as being of the ordinary four-sporangiate type. The writer finds his results agreeing with the later descriptions. In the sections of young anthers there are four distinct sporangia present from the outset of development (fig. 1).

Carpellate flowers

The carpellate flowers occur in compact cymelike inflorescences, several cymes in the axil of each leaf of the flowering branch.

Each flower is subtended by a hood-shaped bract, in the axil of which it arises. This bract, in early development, completely incloses the carpel and perianth (figs. 8, 12, 24).

When first observed, the young female flower consists of a short oblique column of tissue which is triangular in cross-section. On the side directly opposite the midrib of the bract the flower is distinctly lower than the sides next to the bract (figs. 8, 10).

PERIANTH.—The first step in the differentiation of the flower is the appearance of a ringlike upgrowth of the marginal portions of each of the faces of the triangular flower rudiment. This upgrowth is the young perianth. In the earliest stages seen this ring is clearly higher on the two faces lying to the right and left of the midrib of the bract. At first the outline of the floral rudiment as seen in cross-section is convex all around (fig. 11). Somewhat later, however, the outer tissue of the rudiment, that is, the tissue of the perianth, becomes much thicker on the three angles of the young flower, and a distinct depression is evident midway of the length of the flower on each side between the two angles (figs. 9, 10 *Po*). The depressed area bounded by the perianth is the wall of the carpel (fig. 17). This growth of the perianth continues from all directions, until in the ripe seed the wall of the carpel is overgrown by the perianth except for a small pore in each of the three flat sides (cf. figs. 9, 10, 25).

The character of the growth of the perianth is very evident from cross-sections (figs. 11 [upper and lower flower], 18) and from longitudinal sections (figs. 12, 14, 22). Only along a narrow strip, up and down each of the three corners of the ovary (figs. 11 [*X*, upper flower], 12 *Y*), and at a likewise narrow circular band around the upper third of the ovary (fig. 22 *Y*), are the tissues of the carpel and perianth continuous with each other.

A delicate vascular bundle is differentiated in the perianth at each of its three corners (figs. 11, 16). This vascular bundle divides into two near the top of the perianth, and these branches turn one to the right and one to the left, and later are found to be joined to an offshoot of a bundle of the carpel that pushes out into the perianth through the zone of attachment near the top of the ovary (fig. 22). The point of emergence of this carpellary bundle

is directly above the pore in the perianth on the flat side of the flower.

The perianth is never conspicuous either for its size or color. It is greenish, slightly yellow, or brown. It contains on its corners 15–20 layers of cells. The cells remain parenchymatous at first, but in the ripe seed they have rather thick walls and dense contents. The cells bordering on the pore become increasingly cutinized as development progresses.

Earlier observations on this ovary are the following: CLARKE (5) describes the female flowers as consisting of three sepals forming a tube not for the most part adhering to the ovary except at its base and apex where it becomes trifid. He says:

> There is a peculiarity occurring in the calyx of *Hedyosmum hirsutum* or an allied species (one of those in which the flowers are inclosed within thickened bracts so compactly that the apex of the calyx and stigma are alone discernible) which is probably quite singular: on removing bracteae, it is found that the calyx does not completely cover the ovary, but has three large loopholes, as it were, so that three flattened sides of the ovary are seen through it, although it is quite continuous at the angles and crowns it with its three segments as in other species.

SOLMS speaks of a triangular ovary and of the perigon as trifid at the apex, with the stigma sometimes alternate with the lobes of the perigon. BAILLON makes the following observation concerning the perianth: "Moreover, the apex of the ovary bears three short, thick, rounded wings alternating with its angles, two anterior and one posterior. Their morphological value is still uncertain." EICHLER speaks of a three-lobed half, or quite superior perigon. BENTHAM and HOOKER describe the tube of the perianth as grown to the ovary. VAN TIEGHEM says: "La fleur femelle, également nue, se compose d'un seule carpelle à style court renfermant un ovule orthotrope pendant; autour de la base du style, la paroi de l'ovaire se renfle quelquefois en trois bosses épaisses (Hed.)." ENGLER describes briefly the female flower as almost tubular and trifid at the corners. CLARKE has given a fuller description of the perianth, and each observer has mentioned some of the facts.

The question now remains as to the morphological nature of the perianth. The occurrence of three vascular bundles in the

perianth at the corners of the ovary, alternating with the three vascular bundles of the ovary itself, suggests that the perianth may be composed of three modified stamens standing one at each angle of the ovary. There is no definite evidence in favor of this view, since the earliest phases of the developing perianth show no essential peculiarities common to the perianth and to the stamens. The difficulty in accepting this homology is found in the unusual development of the upper portion of the perianth, the tissue of which in the earliest observed stages was in direct continuity with that of the ovary. In favor of such a view as just mentioned, perhaps, is ENGLER's statement that the stamens of *Chloranthus inconspicuus* Sw. are united with a somewhat similar structure extending upward beyond the ovary about one-half its circumference.

Here also must be mentioned the fact that EICHLER (**6**, p. 7, in fig. 3 *B* and *C*) shows in *Chloranthus inconspicuus* an additional structure outside the three stamens, which he designates as a perianth. He says: "Das unterständige Ovar trägt an dem der Braktee zugekehrten Rande ein kleines, mehr weniger herablaufendes Schüppchen, das gewöhnlich als Andeutung eines Perigons betrachtet wird, und innerhalb dieses ein der Axe zugekrümmtes grosses dreilappiges Gebilde, das Androecium." Which of the two structures mentioned compares most closely in origin with the perianth of *Hedyosmum* must be determined by a study of the development of these structures in *Chloranthus*.

It seems clear from the preceding that the origin and growth of the structure termed perianth in *Hedyosmum*, especially in the presence of the lateral pore, differs from that of the perianth of any other angiosperm so far as is known to the writer.

OVARY.—The initial stage in the development of the ovary is that of a convex mass of cells (fig. 7). The outer margin of this dome of cells soon begins to grow more actively, thus leaving a depression in the center of the originally convex mass of cells (fig. 8, flower on left). The rapidly upgrowing ring of cells forms the wall of the ovary, while the central depression which is thus left at length becomes the ovarian cavity (figs. 8, 13, 18). By the continued upgrowth of the carpellary tissue about this depression, the ovarian cavity becomes deepened (figs. 13, 14 *OvC*).

Meanwhile the single nucellus of the ovary grows downward from one side (fig. 14), thus making the ovarian cavity appear crescentic in its upper half when seen in cross-section (fig. 18). This cavity in the lower portion about the hanging micropylar end of the ovule is completely circular in form (fig. 11 *OvC*, upper flower).

With the further growth of the ovary the ovarian cavity is extended upward by the stylar canal which opens out on the side of the style opposite the subtending bract (figs. 14 *SyC*, 22). The lower part of this ovarian cavity at the time the embryo sac is mature extends downward as an inverted conical chamber for half the distance to the base of the ovary (fig. 22). During the maturing of the fruit the cavity is filled by the single seed (fig. 42).

The style and stigma are developed by the continued growth of the upper margin of the carpellary ring, after the latter has closed together above the ovule to form the distinct stylar canal (figs. 14, 22). The stigma is formed solely from the longer lip of the upgrowing carpel (fig. 22). It consists, at the time of pollination, of a flattened triangular surface, the cells of which are parenchymatous. Later, in the ripe fruit, the mature stigma shrivels and disappears. The style is rather short. Internally it consists of two or more layers of elongated cells of small diameter which border on the stylar canal and probably serve as conducting tissue for the pollen tube (fig. 22). Around these layers of conducting tissue are 15 layers of other cells.

Early in its development the wall of the ovary consists of about 10 layers of cells (fig. 14). At the time the embryo sac is ripe the ovarian wall opposite the pore of the perianth is often 15 cells in thickness. Of the 15 layers of cells constituting the ovarian wall, only the 7 outer ones are appreciably specialized in structure. The epidermis becomes gradually cutinized as the embryo sac matures, and papillose cells arise in the exposed area where the perianth does not at first cover the carpellary wall. The cutin layer on the walls of these cells is thickest opposite the pore in the perianth, and becomes gradually thinner in the epidermal cells farther away from it.

At this stage, also, the 6 layers of cells within the epidermis of the ovary are strikingly irregular in contour. The 3 layers immedi-

ately adjoining the epidermis possess irregular cell contours, but their walls are not thickened. They are narrow and elongated. In the nearly mature seed they are not distinguishable from the epidermis, which is non-staining and presents a gelatinous appearance. The next 3 layers of cells adjoining these are thin in radial direction, while tangentially and longitudinally they are of considerably greater dimensions. By far the most salient peculiarity of these cells is the uneven thickening of the walls, which, when first appreciably thickened, are 2–3 μ thick. In the mature seed they are 7–8 μ thick. In the latter case the entire cell cavity is occluded and there is no trace of a nucleus, whereas in the younger ovary, with slightly thickened walls, the nuclei are distinct and remain so until the 10-celled stage of the embryo. The uneven thickening is shown in places by relatively large pits or thin areas (fig. 23 *Pi*). The substance constituting the thickened portions of this wall was found to be cellulose or a cellulose-like substance. These 3 layers of thickened cells doubtless serve to protect the seed. The remaining tissue of the ovarian wall, aside from the vascular bundles, consists of thin-walled parenchymatous cells.

Just within the layers of thickened cells the primary vascular bundles of the carpel are found. There are three of these, one growing up from the base of the ovary along the middle of each flat face (figs. 11 *VB*, 21 *VB-ov*, 42). These bundles are laid down very early in carpellary development and extend for a considerable distance into the tissue of the bract. These bundles extend upward in the wall of the ovary to the level of the chalaza of the ovule, where each bundle divides into two. One of each of these turns inward and bends downward to enter the base of the ovule (figs. 21, 22). From one or perhaps sometimes from each of the three nucellar branches there arises a strand which passes upward to form the single vascular bundle of the style. The second branch of each of the primary carpellary bundles turns outward, away from the nucellus, and passes out from the tissue of the carpel into the perianth through the zone of attachment near the top of the ovule, where the tissue of the carpel and perianth are continuous (figs. 14, 21, 22). Immediately after entering the perianth this perianth branch of the carpellary bundle turns upward to

end in the terminal lobe of the perianth. At either side as it turns
upward this branch is joined by a branch from the perianth
bundle itself (fig. 21 *x*). The presence in the wall of the ovary
of 3 distinct bundles lends strong support to the view that the ovary
is made up of 3 carpels, although no evidence of separate lobes
could be distinguished at the upgrowing margin of the young
ovary.

OVULE.—The nucellus of the ovule is initiated by the inward
and downward growth, on the side opposite the bract, of the subepi-
dermal cells of the wall of the ovary which border on the ovarian
cavity (figs. 14, 18). The integuments arise soon after the carpel
has closed in above the ovule to form the style and stigma. The
inner integument starts as a ringlike outgrowth from the sides
of the ovule near its middle. This is due chiefly to the activity
of its epidermal cells (fig. 26). Soon after the inner integument
appears, a second outgrowth slightly anterior to its base leads to
the development of the outer integument (figs. 26 *OIn*, 28). These
ringlike outgrowths continue growing downward around the
ovule, that is, toward the micropyle, as it elongates. By the time
the tapetal cell has divided, producing the 4 or 5 layers of cells
constituting the tapetum, and the megaspore mother cell has come
to occupy a central position within the nucellus, the inner integu-
ment has completely closed together above the nucellus to form the
micropyle (fig. 28). The inner integument is longer than the outer
from the outset of its development. At the time the embryo sac
is ripe, the integuments extend considerably beyond the nucellus
into the ovarian cavity, and each is 3 cells in thickness. From
this time on neither the integuments nor nucellus change appre-
ciably in appearance until the developing endosperm crushes them
against the wall of the ovary where the integuments form the
seed coat (fig. 42).

The 3 vascular bundles of the ovary can be distinguished
entering the base of the nucellus almost immediately after its
initiation (fig. 11, lower flower). The vascular bundle (indicated
by dotted line in fig. 14) consists of cells which are elongating
actively toward the nucellus, but the walls of which have not yet
begun to thicken. When the embryo sac is mature the nucellus

consists of 7 or 8 layers of cells between the walls of the embryo sac and the outer surface of the nucellus.

The nucellus in the mature seed has been completely absorbed by the swelling endosperm, and there is left only the crushed remains of its cells against the two integuments, the inner of which is considerably thickened in the micropylar region (fig. 42).

Embryo sac

ARCHESPORIUM AND TAPETUM.—Of the group of hypodermal cells seen in the young ovule at the beginning of its development, two axial cells become distinguishable, owing to their larger size and larger nuclei, at the time the outer integument is clearly evident (fig. 26). These two cells are the parietal or tapetal cell above and the definitive archesporial or megaspore mother cell toward the chalaza (fig. 26). The tapetal cell divides early to form the 4 or 5 layers of parietal tissue found in the young seed above the sac (figs. 27–29). The cells of the tapetum thus formed do not change appreciably until crushed by the growth of the endosperm after the formation of the embryo.

The definitive archesporial cell is now considerably elongated and contains a large nucleus (fig. 28). This divides in the usual way to form 3 or more (frequently 4) potential megaspores, as is evident from the condition seen in figs. 29 and 30. The chalazal megaspore of the group is the one which becomes the functional megaspore and develops into the embryo sac, while the 2 or 3 micropylar ones degenerate and are later absorbed (figs. 29–31). The functional megaspore increases steadily in size during the degeneration of the non-functional megaspores, and then evidently begins to divide in the usual way, giving rise to 2, 4, and 8-nucleate stages. The first division of the mother cell nucleus was not observed, but the position within the embryo sac of the nuclei of its second division indicates a definite polarity after the first division, which is evidently maintained on through the subsequent divisions (figs. 31, 32).

The mature embryo sac is of the 7-nucleate type common to most angiosperms (fig. 33). The embryo sac continues to increase greatly in size, and the egg apparatus and endosperm nucleus are

seen to occupy typical positions within it (fig. 34). The endosperm nucleus at the time of its formation by the fusion of its polar nuclei and for some time thereafter contains two nucleoli. Later, however, but a single large nucleolus is visible (figs. 34, 35).

FERTILIZATION.—The writer has not investigated the details of the germination of the pollen grain upon the stigma, nor of the penetration of the pollen tube through the style into the ovarian cavity. From what was observed, it appears that the pollen tube enters the embryo sac in the usual way, displacing and disorganizing the synergids (figs. 35, 37).

The relative time of fusion of male nucleus with the egg was not determined with certainty, but it probably remains for some time in close proximity to the egg without fusion, during which time the endosperm nucleus proceeds to divide actively. The first division of the endosperm nucleus is followed immediately by the formation of a cell wall (fig. 36). Hence it may be said that the endosperm is "cellular from the outset of its development" (JOHN-SON **9**). The egg in *Hedyosmum nutans*, even when the endosperm has reached the 4-celled stage, is still undivided and uninucleolate (fig. 37). In *Hedyosmum arborescens* the fertilized egg is still undivided and binucleolate when the endosperm has reached the 10–12-celled stage (fig. 38). In the earliest stages of the 2-celled embryo seen, the number of endosperm cells is approximately 100. The endosperm continues to divide by longitudinal and transverse walls and rapidly encroaches on the substance of the nucellus (fig. 41). In the mature seed the endosperm has completely crushed and absorbed all but one layer of the nucellar tissue, so that the endosperm lies practically in contact with the inner integument (fig. 43). The antipodals persist unchanged for some time, but as the division of the endosperm continues they begin to degenerate, and finally disappear altogether. The embryo develops into a slightly elongated or oval mass of cells with a poorly developed suspensor (fig. 43).

The chief protection of the seed, except near the micropylar end, where the inner integument is considerably thickened, is afforded by the peculiar thick-walled, pitted cells of the carpel

(figs. 22, 23, 42). The ripe seed is somewhat oval in side view, but sharply triangular in cross-section.

Germination of seed

Observations of the germination of the seed were made in this laboratory by JOHNSON. It is of the type commonly occurring in endosperm-containing angiosperms. The small globular embryo differentiates gradually, and as the hypocotyl grows out of the nucellar region the cotyledons are extended on into the endosperm toward the chalaza. Here they remain until the stored food material is practically exhausted (fig. 44). Later they become freed from the endosperm, expand, and assume active photosynthetic functions.

Discussion

Certain peculiarities in the structure and development of the reproductive organs of *Hedyosmum nutans* which have been described suggest certain conclusions which may be drawn as to its phylogenetic origin. Correlated with these is the question of the comparative primitiveness of this plant in relation to other members of its family and order, and to other angiosperms.

CAMPBELL (3) has studied *Peperomia pellucida*, and JOHNSON has made detailed studies of this and 4 other species of the Piperaceae, as well as of representative genera of the other 3 families of the Piperales. Both investigators have called attention to certain facts bearing also on the relationship of the Chloranthaceae. It is on the basis of the views of these earlier investigators that the writer attempts to interpret the peculiarities occurring in *Hedyosmum*.

An interesting feature of the reproductive structures of this plant is the difference in character of the staminate and pistillate inflorescences. Whereas the staminate flowers occur in long-stalked ovoid catkins (see ENGLER and PRANTL 7, fig. 13), the pistillate flowers, on the contrary, occur in sparsely flowered panicles. The occurrence of these two distinct types of inflorescence, along with the differentiation of the flowers into strictly staminate and pistillate ones, is to be noted in contrasting the

plants of this family with the other 3 families of the Piperales. In all three of the latter, the Saururaceae, Piperaceae, and Lacistemaceae, the flowers are hermaphrodite (except in *Piper Betel* L. var. *monoicum* C.DC. according to JOHNSON **10**, p. 716) and are arranged in distinct catkins. The occurrence of unisexual flowers is generally regarded as a mark of specialization within the family or order, and their presence in *Hedyosmum* indicates that this is one of the more specialized Piperales, rather than a very primitive one.

Again, the perianth of *Hedyosmum* is not of a primitive type. In fact it is a very unusual one. In so far as the writer has reviewed the literature on angiosperms in general, and the Piperales in particular, he has not discovered any type of floral envelope which is at all closely similar to it in its origin or mature structure.

CLARKE, who was the first to describe this perianth and to note its pores, does not discuss its origin, but refers to it as a calyx. SOLMS mentions a structure which he denotes as a perigon trifid at the apex. BAILLON says the apex of the ovary bears 3 short, thick, rounded wings whose morphological value is still uncertain. EICHLER speaks of a 3-lobed half or quite superior perigon. BENTHAM and HOOKER mention a tube of the perianth as grown to the ovary.

The endosperm, which is cellular from the outset of its development, finds its parallel in this respect in *Heckeria* and *Peperomia*, but differs from that of *Piper* (JOHNSON **8, 10**), the only other genus of Piperaceae whose development is known. Elsewhere among dicotyledons the type of endosperm formation found in *Hedyosmum* occurs only in highly specialized forms (JOHNSON **9**). The families in which this is found are placed by ENGLER in the higher orders of the Archichlamydeae and Metachlamydeae. It would seem, therefore, that the conclusion reached by HOFMEISTER, STRASBURGER, and HEGELMAIER, that the structure and development of the gametophyte of angiosperms are not a satisfactory index of broader genetic relationships, finds support here in this peculiarity of the structure and development of the perianth and endosperm of *Hedyosmum*.

Other peculiarities of endosperm development, however, such as the complete replacement of nucellar tissue by endosperm, occur more constantly throughout large groups than such features as a single type of tapetum or embryo sac, or of a particular number of potential megaspores.   These peculiarities, therefore, may have considerable weight in determining such broader relationships.

Summary

1. The staminate flowers usually occur in long-stalked ovoid catkins which arise in a pair at the base of the cymelike female inflorescence.   Each stamen possesses 4 distinct microsporangia.

2. The carpellate flowers occur in sparsely flowered panicles. They have a single pistil, although there is some evidence that 3 carpels enter into the formation of this pistil (5).   The perianth of the female flower is initiated before the carpel.   It is connected with the surface of the ovary by means of a narrow longitudinal band of tissue which extends along each of its 3 corners; by a similar narrow zone about its base; and by another zone of attachment around the ovary in the apical region just below the base of the style.   The perianth persists in the mature fruit and probably constitutes an added protection to the seed.

3. The ovary is 1-celled.   Its wall is composed of 15 layers of cells of which the epidermis and the next 3 layers within it are small and but slightly thickened.   The cell walls of the fifth, sixth, and seventh layers adjoining the 4 just mentioned are at first unevenly thickened, then, during the ripening of the seed, the entire cavity of each of the cells becomes filled.   The inner layer of cells of the ovarian wall next the seed is also considerably thickened in the ripe seed.   These 3 thickened layers form the chief protection of the ripe seed.

4. The ovule is pendulous and orthotropic.   It bears 2 integuments, the inner being the longer from the outset of development. These are quite thick in the mature seed around the micropylar region, but elsewhere they are unthickened and are scarcely discoverable in the mature seed.

5. A primary archesporium arises from a hypodermal cell of the nucellus, which by dividing produces a tapetal cell and a

definitive archesporial cell. The latter divides into three (usually four) potential megaspores. The lower or chalazal one of these is the functional one, the remaining three degenerate and are absorbed. The mature 7-nucleate embryo sac is of the type most characteristic of angiosperms.

6. The endosperm nucleus, embodying two polar nuclei and possibly a male nucleus, begins to divide before the oospore. Its first division is immediately followed by a transverse wall which divides the embryo sac into upper and lower cells. Each of these two cells continues to divide repeatedly, thus forming the thousands of endosperm cells that completely fill the mature seed except for the embryo. The several layers immediately surrounding the embryo are at this time devoid of starch.

7. The fertilized egg begins to divide only after 15–20 endosperm cells have been formed. The synergids and antipodals degenerate by the time of the first division of the oospore.

8. The ripe seed consists of a globular mass of cells with a poorly developed suspensor. The seed coat is not developed appreciably Its function is obviously performed by the wall of the ovary.

9. At germination the small embryo is for a long time inclosed and nourished by the swelling endosperm. The cotyledons remain in the endosperm until nearly all its starch is exhausted. They are then withdrawn and assume an active photosynthetic function.

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EXPLANATION OF PLATES XXXIV–XXXVI

All figures are camera drawings from microtome sections except figs. 9, 10, 24, and 25. Abbreviations used: *Ant*, antipodals; *Br*, floral bract; *EdN*, endosperm nucleus; *Em*, embryo; *Esp*, endosperm; *Fl*, flower; *In*, integument; *IIn*, inner integument; *MN*, male nucleus; *MMC*, megaspore mother cell; *OC*, oil containing cell; *OIn*, outer integument; *Osp*, oospore; *OvC*, ovarian cavity; *PC*, perianth cavity; *Pe*, perianth; *Pi*, pits; *Po*, pore; *PT*, pollen tube; *Sg*, synergid; *SyC*, stylar canal; *Tp*, tapetal cell and tapetum; *VB*, vascular bundle; *VB-ov*, *VB-nc*, *VB-pe*, *VB-sy*, vascular bundles of ovary, nucellus, perianth, and style; *WO*, wall of ovary.

FIG. 1.—Transverse section of stamen showing 3-layered wall, tapetum, and young pollen mother cells; ×110.

FIG. 2.—Detailed drawing of archesporium of one microsporangium with tapetum, etc., shown in fig. 1; ×650.

FIG. 3.—Tetrad of young pollen grains; ×1230.

FIG. 4.—Transverse section of nearly mature anther; ×110.

FIG. 5.—Section of mature pollen grain; ×1100.

FIG. 6.—Polar view of wall of mature pollen grain; ×1100.

FIG. 7.—Longitudinal section of young female flower and bracts; ×55.

FIG. 8.—Similar section of two flowers, upper slightly older than one shown in fig. 7; ×55.

FIG. 9.—Surface view on one side of a young female flower; ×55.

FIG. 10.—Surface view of one side of older female flower; ×55.

FIG. 11.—Transverse section of female inflorescence showing various early stages in carpellary development; ×50.

FIG. 12.—Longitudinal section of female inflorescence; ×50.

FIG. 13.—Similar section of very young flower showing initiation of ovarian cavity; ×550.

FIG. 14.—Similar section at later stage showing initiation of style and stigma; ×250.

FIGS. 15–20.—Successive transverse sections (numbered from base to apex) of single young female flower and subtending bract; ×55.

FIG. 21.—Diagram of wax model of vascular bundle system of perianth and ovary.

FIG. 22.—Longitudinal section of flower at time of ripe embryo sac; ×60.

FIG. 23.—Tangential section of one of thickened pitted cells of ovarian wall; ×70.

FIG. 24.—Surface view of young inflorescence showing bracts and two young flowers; ×20.

FIG. 25.—Surface view of ripe fruit; ×20.

FIG. 26.—Nearly longitudinal section of young ovule showing tapetal and definitive archesporial cells; ×650.

FIG. 27.—Similar section showing inner and outer integuments, origin of tapetum, and increase in size of megaspore mother cell; ×650.

FIG. 28.—Similar section of ovule at still later stage showing inner integument closed above nucellus to form micropyle; ×650.

FIG. 29.—Longitudinal section of nucellus showing young embryo sac with 2 degenerating megaspores above it; ×600.

FIG. 30.—Similar section at later stage showing embryo sac and 3 degenerating megaspores; ×600.

FIG. 31.—Similar section of older nucellus showing polarity of 4-nucleate embryo sac; ×600.

FIG. 32.—Longitudinal section of embryo sac showing mitosis in division of 4 nuclei like those shown in fig. 31; ×1100.

FIG. 33.—Similar section of a mature 7-nucleate embryo sac; ×570.

FIG. 34.—Similar section of micropylar half of mature embryo sac showing typical position of egg apparatus and uninucleolate endosperm nucleus; ×570.

FIG. 35.—Similar section of embryo sac after pollen tube has entered; ×570.

FIG. 36.—Longitudinal section of embryo sac showing first two endosperm cells; ×600.

FIG. 37.—Similar section showing further division of endosperm and antipodals still persistent at base of embryo sac; ×600.

FIG. 38.—Similar section of *H. arborescens* at slightly later stage than shown in fig. 37; ×600.

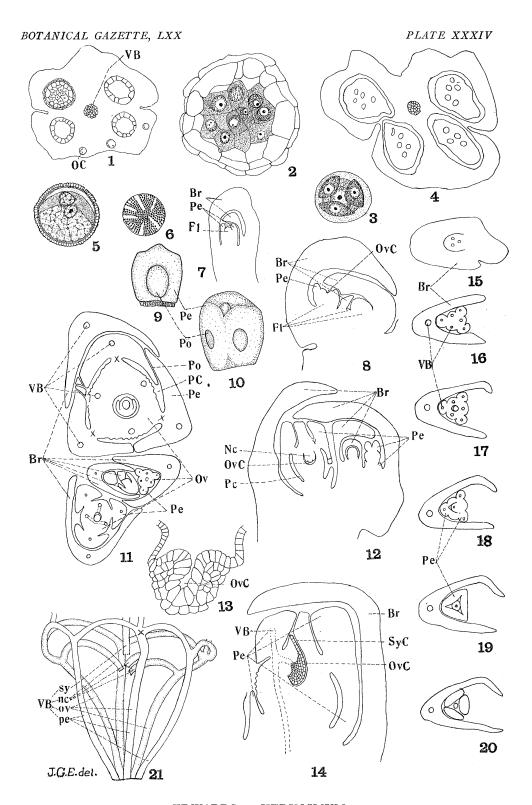FIG. 39.—Similar section of micropylar portion of embryo sac at 3-celled stage of embryo; ×500.

FIG. 40.—Drawing of similar section at later stage showing embryo; ×500.

FIG. 41.—Longitudinal section of micropylar end of nucellus and embryo sac showing character of endosperm around embryo; ×650.
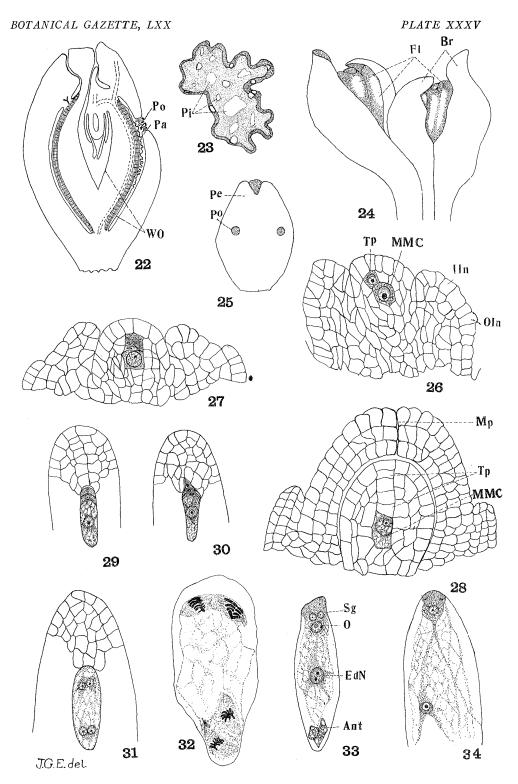
FIG. 42.—Longitudinal section of nearly mature seed showing embryo, endosperm, remains of nucellus, and surrounding wall of ovary with protective cells and still persistent perianth; ×60.

FIG. 43.—Similar section of nearly ripe seed showing embryo, endosperm, and one integument at micropylar end; ×125.

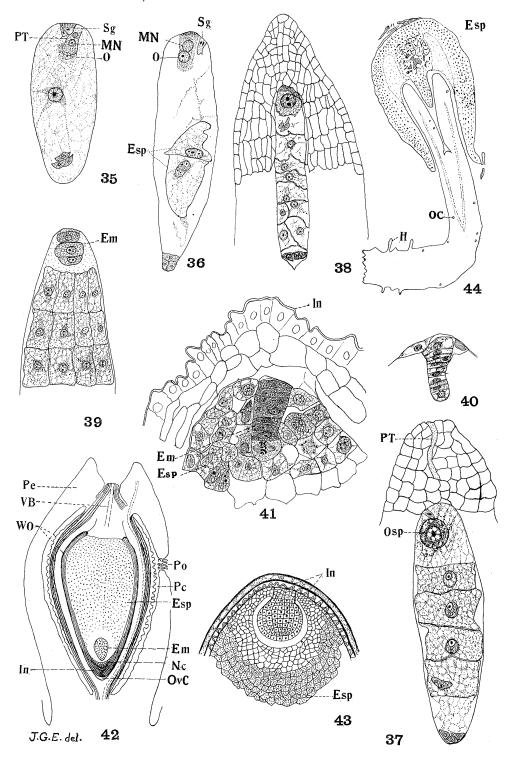FIG. 44.—Longitudinal section of germinating seed removed from fruit showing absorbent cotyledons still imbedded in endosperm; ×60.

PLATE XXXV

J.G.E. del.

EDWARDS on HEDYOSMUM